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A MORPHOLOGICAL STUDY OF CERTAIN ASCLEPIADACEAE.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XLI.

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(WITH PLATES XIII–XV)

IN a previous paper (7) the results of a study of the pollen of certain Asclepiadaceae were published, and during that investigation the remarkable structure of some of the floral organs attracted attention. The present paper is the result of their study.

The species studied were *Asclepias Cornuti* Dec., *A. Sullivantii* Engelm., *A. rubra* L., *A. phytolaccoides* Pursh, *A. tuberosa* L., *A. incarnata* L., *A. obtusifolia* Michx., *A. verticillata* L., *Acerates longifolia* Ell., and *A. viridiflora* Eaton. The material was all collected in the vicinity of Chicago, and in the field plunged into weak chromo-acetic acid. The safranin, gentian-violet, orange combination proved to be the best stain for critical work, although it was often better to omit the orange. The stages were most completely followed in *A. Cornuti*, and the following account applies to it unless otherwise stated. The chief difficulty lies in the small size of the embryo sac. *A. Sullivantii* is a better form, since it has a larger flower, but it was not found in time for young stages. The other species were examined for comparison, and show essential similarity; but any important disagreement is noted.

The family has received considerable attention, but aside from taxonomy most of it has centered about the latex and the pollinia. Chauveaud is the only recent writer who has examined the embryo sac. The latex will not be considered in this paper, except incidentally; and pertinent literature will be noted under the different topics. Schacht (10) states that in *A. Cornuti* the primordia of each set of floral members arise simultaneously and separately, while the sets arise in centripetal succession. Chauveaud (3) reports the centripetal order in *Cynanchum* L. (*Vincetoxicum* Moench). Payer[1] is referred to in this connection, but his book was not accessible.

From the upper surface of the somewhat swollen mass of meristematic tissue destined to bear the flowers of the umbel many hemispherical projections arise, each of which gives rise to a single flower. The outer ones are the first formed. This agrees with the centripetal order of opening of the buds in the umbel. Each flower grows from the axis of a bract which slightly precedes it in origin. One might expect that a careful investigation of an hypogynous, apocarpous, actinomorphic, almost polypetalous flower would reveal its acyclic ancestry, but in no case could any precedence be noted among members of the same set, nor any confluence of primordia. The umbels in *A. tuberosa* are terminal, as shown by longitudinal sections through the stem tip (*fig. 1*), and the same is probably true of the other species.

About the time the carpels appear, the calyx begins a growth of epidermal hairs (*fig. 2*), mostly on the dorsal surface. Later, when the sepals are reflexed, hairs are also formed on their ventral surfaces, which are then exposed. The sepals are reflexed with the petals at the time of the opening of the bud, but after the latter drop off, the former fold tightly up against the carpels. In this second closing their function is again probably protective. The reflexion of the sepals and petals seems to be due to turgescence of cells on their adaxial sides near the base. It is suggested that perhaps the exposure of the adaxial surface of the basal part of the sepals, due to the dropping off of the corolla, causes loss of turgescence and consequent infolding.

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[1] Traité d'organogénie comparée de la fleur. Paris. 1857.

The glands do not seem to have been observed by Schacht (**10**), although they are easily seen with a hand lens. Chauveaud (**3**) saw them within the calyx of Cynanchum, and gives their structure and formation without attempting to explain their function or stating their number. Schumann (**11**) in characterizing the genus Asclepias says the glands within the calyx are paired or single, but makes no mention of their occurrence elsewhere on the plant.

In all the species studied, between the calyx and corolla and alternating with the members of the former, groups of glands were found. In the mature flower there are from one to six in each group, the number and size varying even in the same flower. Usually they are side by side (*fig. 5*), but sometimes they are radially placed (*fig. 6*). They are also scattered singly on the swollen top of the common peduncle. Near the base of a bract of the involucre on its adaxial surface as many as a dozen may be found (*fig. 7*). Dr. H. C. Cowles called my attention to their presence in *A. Sullivantii*, in the axils of the leaves, and and also near the base of the lamina on the adaxial surface of the midrib. I have observed them at the latter point in herbarium specimens of *Asclepias speciosa*, *A. exaltata*, *A. Sullivantii*, *A. Cornuti*, *A. jaliscana*, *A. arenaria*, and would not be surprised if careful examination revealed them in many others.

Taking the development of the glands inside the sepals as an illustration, they appear about the time the carpels begin to show, but on other parts of the plant they appear earlier. At first there is only one representing each group, and it arises from the sepal on its adaxial surface quite near the base and lateral edge. Later others appear on each side of the first and thus the group is formed. The middle (oldest) ones usually remain the largest. In their formation (*figs. 3, 4*) the division of the hypodermal cells forms a protuberance of isodiametric cells over which the epidermis continues. The elongation of the interior cells then increases the length of the protuberance, while the epidermal cells elongate radially over the whole or a part of the surface and function as gland cells, as is shown by their deep stain, volume of protoplasm, and large nuclei (*fig. 8*). These glands are almond-shaped, the flattening being due probably to pressure, since those on the end of the common peduncle are cylindrical. The base is more or less narrowed into a stalk; and those in the axils of the bracts are two or three times as long, proportionally narrower, and more distinctly stalked. Sometimes the epidermis at the tip is not glandular. Some of those on the end of the common peduncle are as much as 1100μ long including the stalk. They remind one here of multicellular glandular hairs. The evidence as to the function of these glands is negative. Their distribution and early appearance precludes the idea of any connection with cross pollination. I have never seen an insect pay any attention to them, although I have often watched for it.

Chauveaud (3) reports that in Cynanchum the corolla, after some elongation, unites with the stamens, but later becomes free. The petals of the species studied are not at any time united with the stamens, although a transverse cut through a bud at an early stage gives such an appearance, because the organs are closely appressed and cut at an angle. At base the corolla forms a short tube, which has probably arisen as a ring from the receptacle. The dorsal surface bears stomata and becomes hairy; and the ventral surface just before the bud opens becomes papillose.

The stamens have been much studied. Schacht (10) gives a figure showing the beginning of hood and horn in *A. Cornuti.* Corry (4) traces the development of the wings in the same species. He also follows the development of the sporangium, wrongly deriving it from a single sporogenous cell. Chauveaud (3) traces the development of the stamen of Cynanchum with its hood or horn, and describes some features in the development of the pollen. Strasburger (14), Gager (8), and the writer (7) have given the history of the microspores. Stephens (13), however, seems to have seen the tetrad divisions; and from an unpublished paper now in my hands it seems that Miss Langley, now deceased, of the University of Michigan, traced correctly the pollen formation in 1897.

The stamens and petals early arise from a common ring slightly elevated above the insertion of the other sets. From the reflexion of the epidermis where the two whorls unite, and from the meristematic character of the cells composing the ring, one is led to conclude that it is of toral origin. The whole stamen in its older stages shows a remarkable tendency to form intercellular spaces, the tissue resembling the spongy parenchyma of a leaf.

The filaments unite to form a ring about the carpels. By their growth upwards against the head the anthers are pushed into a lateral position (*figs. 9–11*). At five points, corresponding to the five lines along which the filaments have united, they do not fit up against the head so tightly. These are the gateways to the stigma.

At the base of the united stamens are two spaces somewhat tetrahedral in form, bounded by the stamineal ring and the two carpels. The general tendency towards the formation of loose tissue expresses itself here in the formation of two protuberances from the base of the stamineal ring, filling these spaces (*figs. 20, 21*) They are large enough to be seen easily with the naked eye and might be taken for rudimentary carpels, but their late appearance and the bulging of the stamineal tissue into them reveals their origin. Eichler (**6**) figures diagrammatically what he calls disk glands in a similar situation in *Vinca minor*. But these projections in Asclepias, while easily mistaken for glands under a hand lens, do not give the dense stain obtained in other glandular tissue of the flower.

Just before the ovules appear, when the pollen has reached the mother-cell stage, the filament pushes out on its dorsal side a crescentic protuberance whose convex side is towards the base, and in whose concavity a papilla appears (*fig. 16*). The crescentic projection is destined to become the hood, and the papilla the horn. The young hood and horn are meristematic at the tip. Spiral vessels appear in the one bundle of each stamen about the time the hood begins to grow. These bend, forming a loop in the hood as it grows larger. When the latter has reached its full development, the vessels extend seven-eighths of the distance to the tip and bend sharply back upon themselves (*fig. 18*). The vessels in the filament must have increased their length, after thickenings had been formed, to at least fifteen times. Whether this was due to the formation of new cells or to the elongation of those present was not determined with certainty, but I am strongly inclined to believe that both things occur. One finds scattered short cells with very close spirals not yet well marked, beside them may be long cells with spirals so long drawn out that their spiral nature is almost lost, the cell walls perhaps even disappearing, the whole showing disorganization. In fact, all the stages in the ontogeny of a vessel may be found in a single longitudinal section of a forming loop. This makes it appear that the spirals form while the cells are not very greatly elongated; that the elongation of the cell takes place by the widening of the part of the wall between the spirals, due either to growth of the cell or to tension arising from the growth of the surrounding tissues; that when the cell has become extremely elongated it collapses and disorganizes, while several cells beside it have meanwhile formed spirals, thus preserving the vascular continuity. Since there is only one bundle in a stamen, the nutrient solutes would find it necessary to pass to the anthers by way of the tips of the hoods. There is no direct connection between anther and pedicel. The tissue of the inner side of the filament forms aerenchyma, thus being able to keep pace with the curving of the bundle without leaving any great hollow. The mature hood is then largely composed of a tissue resembling the spongy tissue of a leaf, but without chlorophyll (*fig. 19*).

The horn is carried up some distance by the growth of the hood, but has no connection whatever with the fibrovascular bundle (*fig. 18*), as one is led to think from one of Schacht's figures. It seems to be built by the division of the cells near its apex, and the later transformation of its tissue into aerenchyma, for its whole interior is filled with very loose tissue (*fig. 19*). In Acerates, as the name implies, there is no horn. However, the bundle passes into the hood as in Asclepias, while in Cynanchum (3) it simply curves into the base of it. The direction of the bundle in relation to the hood may prove to be of value in determining relations among the Asclepiadaceae.

The hood and horn are known to enclose the nectar, but the part played by the horn in pollination is not clear.

The formation of the anthers, with their wing-like projections and two sporangia, as well as the development of the microspores, has been worked out by the writers referred to above. In general, the account is the same for all the species examined.

The development of the male gametophyte is pretty well known. Corry (5) saw the generative and tube nuclei in *A. Cornuti*, but supposed the larger to be the generative cell. Strasburger (14) found the small one to be the generative cell, and the writer (7) found the same in *A. tuberosa.* Gager (8) observed the first division of the microspore in *A. Cornuti*, and the division of the generative nucleus.

A. verticillata proved to be the best form for the study of the pollen grain, and hence it is here taken as the type, although the others agree with it in general features. The generative cell, flattened out against the wall usually in lenticular or hemispherical form (*fig. 22*) and varying in size, soon loosens and approaches the tube nucleus (*fig. 23*). The two nuclei are greatly different in size and both have the chromatin in granular threads. The generative nucleus usually has massed about it a quantity of denser cytoplasm of finer structure and bounded by a definite wall. The wall sometimes persists until division is complete (*fig. 26*), and at other times division follows its resorption (*figs. 24, 25*). The lenticular form is gradually changed to crescentic, oval, or even spherical. The division forming two male cells occurs about the time the buds open. It is not quite simultaneous in the same anther, although the amount of variation is not great. In all cases observed, division occurs near the tube nucleus. In *fig. 25* eight chromosomes were counted, but not with absolute certainty. Those in the vegetative cells of the stamens are about the same in number, contrary to expectation, but they are so extremely small that a definite statement is not warranted. The condition of the cytoplasm in the pollen grains of the same anther seems to vary. In some it is reticulated, in others homogeneous. In almost all one finds groups of the deeply staining bodies of undetermined nature (*fig. 24*). In

A. verticillata they are almost spherical. The determination of their nature has been left to Mr. Gager, who announces work in progress on them. I have found bodies in *A. tuberosa* in the latex tubes resembling those in the pollen of that species in staining properties and in form, thus adding weight to the food theory. In some pollen grains there are single spherical bodies of varying size, resembling those in the groups in their staining capacity (*fig. 25*).

Concerning the pistil Schacht (**10**) states that the two carpels roll in adaxially, each forming a loculus, while the fusion of their tips results in the head (Corry's "style table"). He also figures an ovule showing a nucellus. Corry (**5**) has gone at length into the formation of the head and especially into the origin of the corpusculum and caudicules. Schumann, however, doubts his conclusions. In regard to the development of the ovules almost nothing has been done except in Cynanchum, in which Chauveaud (**3**) reports that there is no nucellus, no integument, and only one megaspore.

The arrangement of the carpels in relation to the outermost sepal seems not to be a constant one, although usually one is opposite. The carpels remain separate except at their tips. The loculus formed by the rolling in of the edges opens in the head a short distance above the stigma. The cleft on the inner surface is never completely lost.

Quite early, before ovules appear, before even the edges of the carpels have rolled in to any considerable extent, the tips of the carpels come in contact and begin fusion, forming the head. This is about the time of the first division of the archesporium in the anthers. The ends of the carpels enlarge enormously, forming a somewhat spherical mass (the head) with a funnel-shaped depression at the top, which is sometimes deep, sometimes shallow (*fig. 28*). The fibrovascular bundles of the carpels flatten out, and by the juxtaposition of their edges form a hollow cylinder in the center. At the apex the cylinder spreads, forming a funnel. Corry (**5**) figures it doubling back towards the base, but diligent search revealed no such case. The stigma has long been known to be situated just beneath the head, although some writers have considered the head stigmatic. Corry (5), limiting the term stigma to that portion fitted for the reception of the pollen, naturally regards the head stylar. One is led to conclude from his statements that he believed the tips of the carpels were abaxially reflexed to the functional stigma, seeing an argument for it in cases of the reflexion of the fibrovascular bundle. The conductive tissue, however, does not follow the path which a definite location in a recurved leaf would give it; and if it is not definitely placed in the carpel, its outcrop, the stigma, is not more definitely located. Those who believed the head to be of stigmatic origin thought the functional stigma to be under the corpusculum. The question here is a phylogenetic one. Has the stigma always been where it now is, the head developing above it later; or, teleologically speaking, has the stigma moved to adapt itself to the modifications of the floral organs? The papillose epidermis of the funnel-shaped depression in the top of the head, the suggestion of conductive tissue in appearance of the cells beneath this epidermis, the absence of a downward curve in the tips of the bundles, and the continuation of the conductive tissue above the functional stigma, all indicate that the homologue of the stigma in other plants is the funnel. We may then regard the head as an abaxial thickening of the style immediately beneath the stigma. We would then have later the formation of a new stigma beneath the head, and the cessation of functional activity in the one at the top. The strongest argument in favor of Corry's theory, however, and one not mentioned by him, is found in the Apocynaceae. Here one finds stigmas on the equator of a fusiform head, a stage between the terminal stigma of the Gentianaceae and the subcapital one of the Asclepiadaceae.

Incidentally, many of the stages in the formation of the caudicules and corpuscula were observed and Corry's account (5) confirmed.

The conductive tissue lines the placenta and the canal that forms the continuation upwards of the cavity of the ovary. Just beneath the head it spreads out as a disk or funnel, reaching the surface in a circle under the head (*fig. 28*). The stigma therefore forms a band completely surrounding the head at that level, but because the upward projections of the styles unite closely with the head, the stigma is accessible only through the alar chambers, corresponding to the intervals between the stamens. The conductive tissue lines the canal to its end.

In the formation of the ovules rounded projections (*fig. 29*) are pushed out in longitudinal rows, the lowest in each row being the oldest. Before there is a distinct differentiation of funiculus, one of the hypodermal cells at the upper outer angle of the ovule can be recognized by its larger nucleus and different stain as an archesporial cell (*fig. 29*). Occasionally one finds two or three archesporial cells side by side (*fig. 30*), but in such cases one seems to outgrow the others, for in no case was more than one in its later well developed stage (*fig. 31*) found in the same ovule. The epidermal layer over the archesporial cell is the only sterile part of the nucellus. Schacht (**10**) figures a nucellus projecting from the ovule like a papilla. Such forms I could not find in *A. Cornuti*, and they must be exceptional. By the cessation of growth in the nucellus, and its continuation around it to form the single integument, the nucellus comes to appear deeply sunken (*fig. 34*). The nucellus is short lived, being very soon replaced by the embryo sac. It seems remarkable that there should be no nucellus or integument in Cynanchum as reported by Chauveaud. If one takes the view that he overlooked an evanescent nucellus his story accords well with that in Asclepias and Acerates, his "revêtement protecteur très épais" becoming the integument. Its appearance and manner of formation are about the same as the integument of the genera studied

The archesporial cell reaches a size equal in section to a dozen of the surrounding cells. No parietal (tapetal) cell is cut off, and by two successive divisions a row of four megaspores is formed (*figs. 32, 33*). This does not always occur during the same stage in the development of the integument, as sometimes it occurs when the nucellus is not yet covered, and at other times when the nucellus is deeply imbedded in the body of the ovule. To avoid confusion the two cells resulting from the first division of the archesporial cell will be called daughter cells.

Both daughter cells and megaspore will be numbered beginning nearest the micropyle.

The number of chromosomes in the division of the archesporial cell could not be determined. In the division of the daughter cells of *A. Sullivantii* five were counted in several cases, but not with certainty. There are approximately half as many, however, as in the vegetative cells. The two daughter cells do not always divide simultaneously. In *A. tuberosa* only one case of this division was observed, and in that they were not widely separated in time, although the micropylar daughter cell was the later to divide, and the spindle in it (*fig. 33*) was smaller. In *A. Sullivantii* many dividing daughter cells were found, and in no case were the divisions in the same ovule simultaneous. In some cases, however, the equality of the megaspores leads one to think that this may sometimes be the case. In the cases observed, the second daughter cell was always the first to divide (*figs. 39, 40*). The difference in time appears to vary, if one may judge from the difference in development of the third and fourth megaspores at the time of division of the first daughter cell. Sometimes the third and fourth megaspores have undergone little change when the first daughter cell divides; sometimes one of the two has considerably enlarged, usually the fourth; and sometimes the third is already largely resorbed (*fig. 39*). The fourth megaspore does not always function as the embryo sac, but any one of the four may, the relative frequency rapidly decreasing from the fourth to the first. All were seen to form sacs in *A. Sullivantii* except the first (*fig. 41*), and very probably that could be found. The first was seen to form the sac in *A. tuberosa* (*fig. 36*). Occasionally one finds two megaspores growing alike (*fig. 37*), but that one is finally crowded out is evident from the absence of more than one mature embryo sac in an ovule. The functioning of other than the most deeply seated megaspore has been reported before in several cases, but its frequency in *A. Sullivantii* is rather remarkable. In perhaps 10 per cent. of the cases observed the fourth megaspore did not become the embryo sac. In *A. tuberosa* and *A. Cornuti* the per cent. is much smaller.

The resorption of the three arrested megaspores takes place rapidly, so that one might easily overlook the stage completely. In *A. tuberosa* the megaspores farthest from the functioning one seems to be resorbed first (*figs. 35, 36*). One would suppose that the nearest would be the first to disappear, for in the disorganization of the surrounding cells those nearest are the first to change. In *A. Sullivantii*, from the cases of disorganization of the third cell while the first and second are still in good condition, one gets the suggestion that before the first daughter cell divides it offers greater resistance to disorganization than it does later. From *fig. 40* one is led to conclude that the first daughter cell before its division either aids in the disintegration of the third megaspore or utilizes its space as the fourth absorbs it.

Among the Asclepiadaceae, therefore, we find one of the strongest arguments for homologizing the row of four cells in the ovule with the tetrad of microspores. It is known (7) that in the formation of microspores each cell of a hypodermal archesporial plate divides, forming a parietal and a primary sporogenous cell. The latter without division functions as a mother cell, which gives rise, with reduction of chromosomes, to a row of four microspores, each of which develops a male gametophyte. In the formation of megaspores usually a single hypodermal archesporial cell does not divide to form a parietal cell, but functions directly as a spore mother cell, giving rise, with reduction of chromosomes, to a row of four megaspores, any one of which may develop a female gametophyte.

But what is the significance of the retardation in the division of the first daughter cell ? No cases of the first preceding the second are reported, and the question as to the origin of this retardation becomes pertinent. In tetrad formation among the pteridophytes the daughter cells divide simultaneously. The possibility of a relation between the retarded division and the suppression of functional activity in three of the four megaspores is suggested. If such a relation exists, there are three possibilities :

1. The suppression of three of the four megaspores may cause the retardation in division of the cell forming two func-

tionless ones. This would presuppose some unknown cause operating to suppress three, probably the same which operates to reduce the number of megaspores in heterosporous pteridophytes. It has been suggested that the central position of the fourth megaspore gives it an advantage over its fellows in food supply. If nutrition is obtained from the resorption of the surrounding cells and the influx of food stuffs, this claim receives added weight when it is remembered that the fourth megaspore is nearest the point where the later formed vessels end. The retardation would then be regarded as the beginning of the suppression of a useless division, The apparent variation in the relative time of division of the two daughter cells adds weight to this view, and cases like *figs. 38* and *39* suggest that there may be here a transition between the row of four and of three. If one were to find a case like *fig. 38* alone, it might easily be mistaken for an example of the formation of only three megaspores; but from the size and appearance of the nucleus of the first daughter cell, and from the fact that such stages must have been passed by *fig. 39*, it seems clear that the first daughter cell would have divided again. But if retardation were more pronounced in a case like *fig. 39*, one can readily see that resorption might occur before the first daughter cell divides, and the condition of three megaspores would be established. It is possible that in some such way the reduction in numbers of megaspores took place in those spermatophytes in which only three or fewer megaspores have been reported.

2. The retardation in the division of a daughter cell may cause suppression of some megaspores. This would presuppose some unknown cause for the retardation. The earlier division of the second daughter cell would no doubt give the third and fourth megaspores an advantage over the first and second, but it would not account for the much more frequent predominance of the fourth than of the third unless the relation to food supply were again introduced.

3. Both retardation and suppression may be due to a common unknown cause.

That retardation in division resulted from loss of function seems to be the most satisfactory hypothesis at present. Since no case of retardation in division of the second daughter cell was observed, it would be interesting to know the relative time of division of the two when the first or second megaspore predominates. Since only one case of the division of the daughter cells was observed in *A. tuberosa*, no conclusions can be drawn concerning the meaning of the smaller spindle in the first.

The embryo sac passes rapidly through the typical two, four, and eight-nucleate stages (*figs. 42, 43*), and the usual ante-fertilization stage of the sac is reached. Occasionally one finds more than three antipodals (*fig. 45*), but it is quite the exception, and only once were fewer than three noted. The synergids resemble the egg very closely in many cases and can be distinguished from it only by the relative nearness of their nuclei to the micropyle (*figs. 43–46*). The number of cells at the micropylar end was constant, although Chauveaud (3) figures five micropylar cells in the sac of Cynanchum, and believed that the five embryos sometimes found were due to the fertilization of all of them. The sac enlarges very rapidly, soon destroying the nucellus and much of the surrounding tissue. In one case noted it had replaced the surface of the ovule (*fig. 44*), while in several instances it had come near it.

In this connection it may be noted that in two ovules a tracheid was observed near the base of the embryo sac and slightly projecting into it, showing that the thickening of their walls had occurred before the sac had reached its full development (*fig. 48*). In only two other genera of angiosperms has the occurrence of tracheids in the nucellus been reported: in Castanea by Miss Benson (1), and in Casuarina by Treub (15). The occurrence of a tracheid near to such a rapidly enlarging embryo sac raises the question whether increased conduction had not been the cause of its formation. That increased conduction leads to increased formation of tracheary tissue seems evident from Vöchting's experiments with the potato and other tubers. That it causes the formation of tracheary tissue where there has been none phylogenetically there is no evidence except in the evolution of vascular from non-vascular plants. Could the tracheids radiating from the base of the ligule in Isoetes (12) have any relation to those in the ovules of Asclepias? In any event, in the ovule one would expect the formation of leptome rather than of hadrome from such a cause. This throws us back upon Miss Benson's (1) suggestion that this is an indication of a degenerate chalazal vascular strand once extending into the nucellus. Judging from the form and arrangement of the cells between the end of the vascular bundle, which appears later, and the sac, the tracheid is just about where the former, extended, would meet the latter. That a primitive feature so nearly lost, even among the lower Archichlamydeae, should appear among the Asclepiadaceae seems remarkable, and suggests a doubt as to its primitive character.

The fertilization of the Asclepiadaceae has long been a subject of interest. According to Corry (5), Robert Brown saw the pollen tubes in the ovary and noticed that they were attached to the ovules, but like all other botanists of his time he supposed the tubes reached the ovary by way of the caudicules and the head. According to Brongniart (2), Ehrenberg rediscovered the tubes, but considered them permanent structures. He observed that the tubes issue from the side of the pollinium, thus disproving the theory of fertilization through the caudicules, and leaving the location of the stigma in doubt. Two years later Brongniart (2) properly located the stigma, and traced pollen tubes from the pollinia into the style. Since he wrote before insect pollination had received much attention, he accounts for the development of the pollen tubes within the anther by the passage of a hypothetical liquid from the corpusculum into the pollinia by way of the caudicules. Whether pollen tubes do sometimes form within the anthers, or whether Brongniart was mistaken in the location of the bursting pollinia is still a matter of doubt. Corry (5) says that flowers artificially pollinated with their own pollen remain sterile, although the tubes penetrate the style. He observed one nucleus, probably the tube nucleus, enter the tube, and traced the tubes to the ovary. Chauveaud (3) reports that in Cynanchum he found pollen grains putting out tubes within the anther. Gager (8) reports that in *A. Cornuti* the tube nucleus enters the pollen tube in advance of the male cells. He found the tubes in the micropyle, and the two male cells, when they reached the ovule, were still spherical and unaccompanied by the tube nucleus.

The pollen tubes penetrate the stigma in a mass and pass down the hollow of the style. All penetrate into the same ovary. The tissue seems to be no obstacle, for they could get into the stylar canal without such penetration by a slightly less direct route. In the ovary they spread out, fan-like, over the surface, forming a mat. To reach the micropyle a tube grows up between the ovules, or when the ovules are somewhat isolated it follows the funiculus, or even passes directly across the cavity to reach its destination. Reaching the sac it usually passes along the inner surface of the wall until it gets above the synergids, where it seems to burst, discharging the contents for some distance into the sac. Sometimes one of the synergids is destroyed, but there seems to be no regularity about it. In *A. tuberosa* the male cells are in advance of the tube nucleus and near the tip of the tube when it penetrates the stigma (*fig. 47*), differing in this respect, according to Gager, from *A. Cornuti*. In their passage down the tube the male cells advance more rapidly than the tube nucleus, so that the latter reaches the upper part of the ovary about the time the male cells enter the embryo sac. The tube nucleus goes no further, and may be found there after the endosperm has begun to form. Experiments with tubes grown in weak sugar solutions show, as one might expect from their delicacy, that the tubes are very sensitive to changes in osmotic pressure. By slight changes one can cause the contents to flow back and forth in the tubes without injuring the walls. The flow can be watched under a compound microscope. When the tubes are burst by too rapidly decreasing the osmotic pressure on the outside the rupture is always at the tip. This raises the question whether in killed material much dependence can be placed upon the position of the nuclei in the tube, either in reference to one another or to the end of the tube. The killing fluid might easily cause flowing and change in position, and the sensitiveness of the delicate tubes to changes in osmotic pressure makes it seem probable that this often occurs. It seems that the normal bursting of the end of the tube after penetrating the embryo sac might be due to the same cause.

The polar nuclei have usually not fused when the tube bursts. The antipodal one is somewhat below the middle of the sac, while the micropylar one is usually somewhat above it (*fig. 48*). Before the polars have fused, one of the male cells unites with the antipodal one, and about the same time the other male cell fuses with the egg (*fig. 48*). The male cells are crescentic in form, reticulated with granules, and not conspicuously unlike in size. In one case a male cell was found fusing with the polars after their union. This does not seem singular, however, when we recall the method of pollination. Insect pollination requires some range in time for the process. Fertilization may then occur at different stages, or the embryo sacs must remain stationary in the proper stage until the male cells arrive. But unfertilized ovaries show that the embryo sacs pass into the seven-celled stage (*figs. 43, 44, 46*); that is, the polars unite whether fertilization has taken place or not. Again, the older ovules are nearer the base of the ovarian cavity, while the pollen tubes enter in a mass at the top. The younger ones it seems, in any given ovary, would be fertilized first, with the result that fertilization in different stages of fusion of polars would occur. In fact, the literature of double-fertilization gives us instances of fertilization before, during, and after fusion of polars, but not all in the same species. The fusion of a male cell with the antipodal polar is characteristic of *A. Cornuti* when fertilization occurs before fusion of the polars; but it is not unique in plants, for Guignard (**9**) reports seeing a case of it in *Lilium Martagon*. He thinks, however, that the male cell goes to the polar nearest it at the time of its issue from the tube. The conditions in *A. Cornuti* make such a theory improbable, at least for that species. The micropylar polar was in all the cases observed nearer the end of the tube than the antipodal (*fig. 48*), yet in all cases of fertilization before polar fusion the male cell fused with the antipodal polar. If the male cells have independent motion, the question arises as to what impels the male cell in one plant to seek the micropylar polar and in another the antipodal. To say that the upper polar has the greater attraction because it is sister to the egg is not sufficient, for in *A. Cornuti* the polar most distantly related to the egg has the greater attraction. Nor will proximity account for it, for the micropylar polar is nearer the end of the tube than the antipodal. It might be supposed that incidentally this lends weight to Strasburger's view that the male cell is carried by the streaming of the protoplasm, but in this case we should have to suppose the streaming to be towards the antipodal polar. If the polars are in any way carried by the stream, we should expect that the streaming would more often be from the end of the tube towards the farthest polar, but that the polars are carried to any considerable extent is doubtful. Another objection is the proximity of the micropylar polar in some cases to the end of the tube. It seems as though the male cell would unite with the micropylar polar if the latter had the same affinity for it as the antipodal polar. On the whole, I am inclined to believe that the antipodal polar has for some unknown reason a stronger attraction for the male cell than has the micropylar.

The sac after fertilization is greatly increased in size by the development of the endosperm. The first division of the endosperm nucleus occurs soon after fertilization, but the actual division was not observed. The second and third divisions rapidly follow, forming eight endosperm nuclei (*fig. 50*). Up to this time the nuclei divide simultaneously and no walls are formed. The number of chromosomes in the endosperm could not be determined, but there were more than in the megaspores. In many cases there was a tendency towards the massing of the endosperm about the egg. The cytoplasm of the sac seems to increase in volume as the number of free nuclei increases. In the eight-nucleate stage of the endosperm the formation of the walls by indentation begins (*fig. 50*). The division into sixteen nuclei seems to be nearly simultaneous, since few cases could be found where there were between eight and sixteen nuclei. By this time the cells have become somewhat walled off (*fig. 51*), and the divisions from this time on are not simultaneous. The antipodals may still be seen flattened out against the sac-walls when there are approximately thirty-two endosperm nuclei (*fig. 52*). Frequently in this stage one of the synergids could still be recognized as a small, poorly staining nucleus, crowded into the space at the base of the egg (*fig. 52*).

The egg after fertilization forms a distinct wall and rests. No division occurs before the endosperm has passed its sixteen-celled stage (*fig. 51*). This leads one to question whether the reported cases of endosperm division before fertilization, *e. g.*, Casuarina (15), may not be due to misinterpretation, the resting egg being mistaken for an unfertilized one.

Some changes of interest occur in the ovule after fertilization. Before fertilization the placenta begins the formation of a longitudinal ridge under each row of funiculi. This continues to grow higher until when the seeds mature it is a membrane about 3^{mm} high. In it can be seen plainly with the naked eye the bundles passing to the ovules. On account of the growth of the lateral portions and ends of the ovules, and possibly pressure from the ovary wall, funiculo-micropylar flattening takes place. It seems that growth along the sides has most to do with the flattening, for the tissue in the edges is quite meristematic. About the time of the third division of the endosperm the epidermis at the micropylar end of the ovule — the one nearest the top of the ovary — becomes intensely active. The cells elongate enormously and form the pappus. The hairs composing it remain single cells with a single nucleus in each. Chauveaud (3) reports two nuclei in each in Cynanchum. The pappus is tightly packed in the grooves between the placental ridges, and the free ends extend towards the apex of the pod. The micropyle in *A. Cornuti* and *A. Sullivantii* is still visible with a hand lens when the seed begins to turn brown. The funiculus never thickens much, so that in its later stages it is little more than a vascular bundle and is very easily broken off.

The changes resulting in the formation of the pod also deserve attention. At or shortly before the time of fertilization, the outer epidermis becomes active, as is shown by its deep stain and protoplasmic contents. The surface usually becomes covered with papillae, specially where the ovary narrows into the style. The papillae in *A. Cornuti* sometimes develop into long finger-like projections, as observed by Brongniart (2), although sometimes they form only rounded knobs. Fertilization causes the rapid development of a dense covering of hairs on the outer surface and sometimes a few on the inner. Each hair is composed of a single row of cells which arises from an epidermal cell. Another result of fertilization is the development of a meristem layer just beneath the inner epidermis. There are signs of this meristem just before fertilization, but it remains only a sign unless fertilization occurs. The result of the activity of this meristem is the rapid thickening of the ovary wall, which is accompanied by the formation of dorsiventral bundles. Preceding fertilization there is in the carpel only one bundle, centrally located. From this other bundles form laterally when pod formation begins, but at first all are parallel to the surface of the carpel. The elongated elements which later form the dorsiventral vessels were first noticed when the endosperm was in the two to eight-nucleate stage. With the formation of dorsiventral vessels there is a rupture of the parenchyma between them, forming cavities. These are well under way by the time the egg undergoes its first division. Further development of the cavities results in the formation of a pod composed of two walls separated by a large space bridged only by bundles with a casing of parenchyma. The cavities extend even into the papillae, which in the mature pod vary from almost nothing to 6^{mm} in length. The dorsal bundles remain closely applied to the dorsal wall of the cavity. The layers of cells next the inner surface become elongated in different directions, forming a firm layer which shows a smooth surface on the side next to the seeds.

SUMMARY.

1. The umbels are terminal.
2. The floral parts appear in centripetal succession.
3. The members of the same set arise simultaneously, and there is no confluence of primordia.
4. Glands are present near the axils of the sepals, bracts, and

leaves, in some species also on the midribs of the leaves; they are not in pairs, as stated by Engler and Prantl; and are not nectariferous.

5. The tube of the corolla seems to be of toral origin.

6. The adaxial surface of the corolla becomes papillose at the time of blooming.

7. The stamens are remarkable in the development of intercellular spaces.

8. The horn and hood are lateral outgrowths from the filament and composed largely of extremely loose tissue.

9. The fibrovascular bundle of the stamen loops into the hood to near its tip, the curvature beginning after the walls of the tracheids have formed spirals.

10. The elongation of the bundle to form the loop seems to take place by the stretching of the old tracheids and the formation of new ones at their sides.

11. The horn contains no vascular tissue.

12. The top of the "head," and not the functional stigma, is believed to be homologous with the stigma of normal angiosperms.

13. In general Corry's account of the formation of the caudicules, or connectors, and corpuscula is corroborated.

14. The generative cell divides near the tube nucleus, and in the normal manner. The division occurs before the formation of pollen tubes.

15. The pollen tubes from the same pollinium all enter the same ovary.

16. When the pollen tube enters the stigma the tube nucleus is behind the male cells, but it is doubtful whether any reported positions of nuclei in pollen tubes are beyond question.

17. The tube nucleus gets no further than the upper part of the ovary.

18. There is a single integument.

19. The nucellus is a single layer of cells enclosing the sporogenous row.

20. A single hypodermal archesporial cell forms a row of four megaspores without the formation of a parietal cell. Occasionally there is more than one archesporial cell.

21. In the formation of the megaspores the daughter cells do not divide simultaneously, thus perhaps giving a clue to the history of the abridgment of the process in some angiosperms.

22. The female gametophyte develops normally.

23. Double fertilization was observed in *Asclepias Cornuti*, one of the male cells fusing with the antipodal polar nucleus. This throws doubt upon the view that the attraction is due to near relation of the micropylar polar to the egg.

24. Fertilization may occur before or after the fusion of the polars.

25. A few tracheids were found in the ovules near the antipodals.

26. The fertilized egg rests until the endosperm has become sixteen-celled or more. It is surmised that some reported cases of endosperm division before fertilization may be due to mistaking fertilized for unfertilized eggs.

27. The pappus is composed of single-celled, uninucleate, epidermal hairs.

28. The double wall of the pod has its origin in the rupture of the parenchymatous tissue within the wall of the carpel.

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EXPLANATION OF PLATES XIII–XV.

All drawings × 23 or more were made with a camera lucida. The lenses used were Zeiss compensating oculars in combination with Leitz dry lenses, a Zeiss dry achromatic adjustable, or a Zeiss $\frac{1}{12}$ apochromatic oil. The original drawings, for which the magnifications are indicated, are twice as large as the reproduction.

Asclepias tuberosa.

FIG. 1. Longitudinal section through stem tip showing terminal umbel; *g*, glands; partly diagrammatic; × 30.

FIG. 2. Hair from the epidermis of the calyx; × 390.

FIGS. 3–4. Glands on the adaxial surface of the calyx; *p*, petal; *s*, sepal; × 555.

FIG. 5. Top view of flower with all its organs removed except the sepals; *s*, sepal; *g*, gland; *p*, where petals have been cut; shows position of glands; × 48.

Asclepias Sullivantii.

FIG. 6. Part of longitudinal section through flower showing three glands in radial relation; *s*, sepal; *p*, petal; *b*, bundle; × 48.

Asclepias Cornuti.

FIG. 7. Basal portion of bract from umbel showing glands on adaxial surface; × 48.

Asclepias tuberosa.

FIG. 8. Gland from receptacle ; *r*, receptacle ; *p*, pedicel ; × 390.

FIG. 9. Young stamen ; *p*, pollinum ; *b*, elongated elements preliminary to a bundle ; × 48.

FIG. 10. Young stamen, older than *fig. 9*; *e*, end of vessel ; *h*, beginning of hood and horn ; × 48.

FIG. 11. Longitudinal section of stamen ; *e*, end of vessel ; *n*, horn ; *d*, hood ; *p*, pollinium ; × 48.

FIGS. 12–15. Cross sections through *fig. 11* in planes indicated; *p*, pollinium ; *c*, corpusculum ; *w*, wing ; *a*, alar chamber ; × 94.

Asclepias Cornuti.

FIG. 16. Dorsal view of young stamen with concentric hood and papillate horn ; × 23.

Asclepias tuberosa.

FIG. 17. Longitudinal section of stamen; hood and horn forming rapidly ; × 23.

FIG. 18. Longitudinal section through mature stamen showing bundle looping far up into the hood ; × 23.

FIG. 19. Section from *fig. 18* through hood (region indicated) showing aerenchyma ; *s*, air space ; × 203.

Asclepias Cornuti.

FIG. 20. Part of flower with slice removed by tangential cut ; *s*, stamen ; *o*, ovary ; *m*, mass arising from the stamineal ring ; × 23.

FIG. 21. Longitudinal section of basal part of stamen ; *s*, sepal; *p*, petal; *n*, stamen ; *m*, mass arising from stamineal ring ; × 94.

Asclepias verticillata.

FIG. 22. Pollen grain ; *g*, generative cell ; *t*, tube nucleus ; *b*, undetermined bodies ; × 1500.

FIG. 23. Generative cell leaving the wall of the pollen grain ; × 1500.

FIG. 24. Generative cell before division, without a wall ; *g*, generative cell ; *t*, tube nucleus ; × 1500.

FIG. 25. Division of generative cell, no wall about it ; × 1500.

FIG. 26. Division of the generative cell ; × 1500.

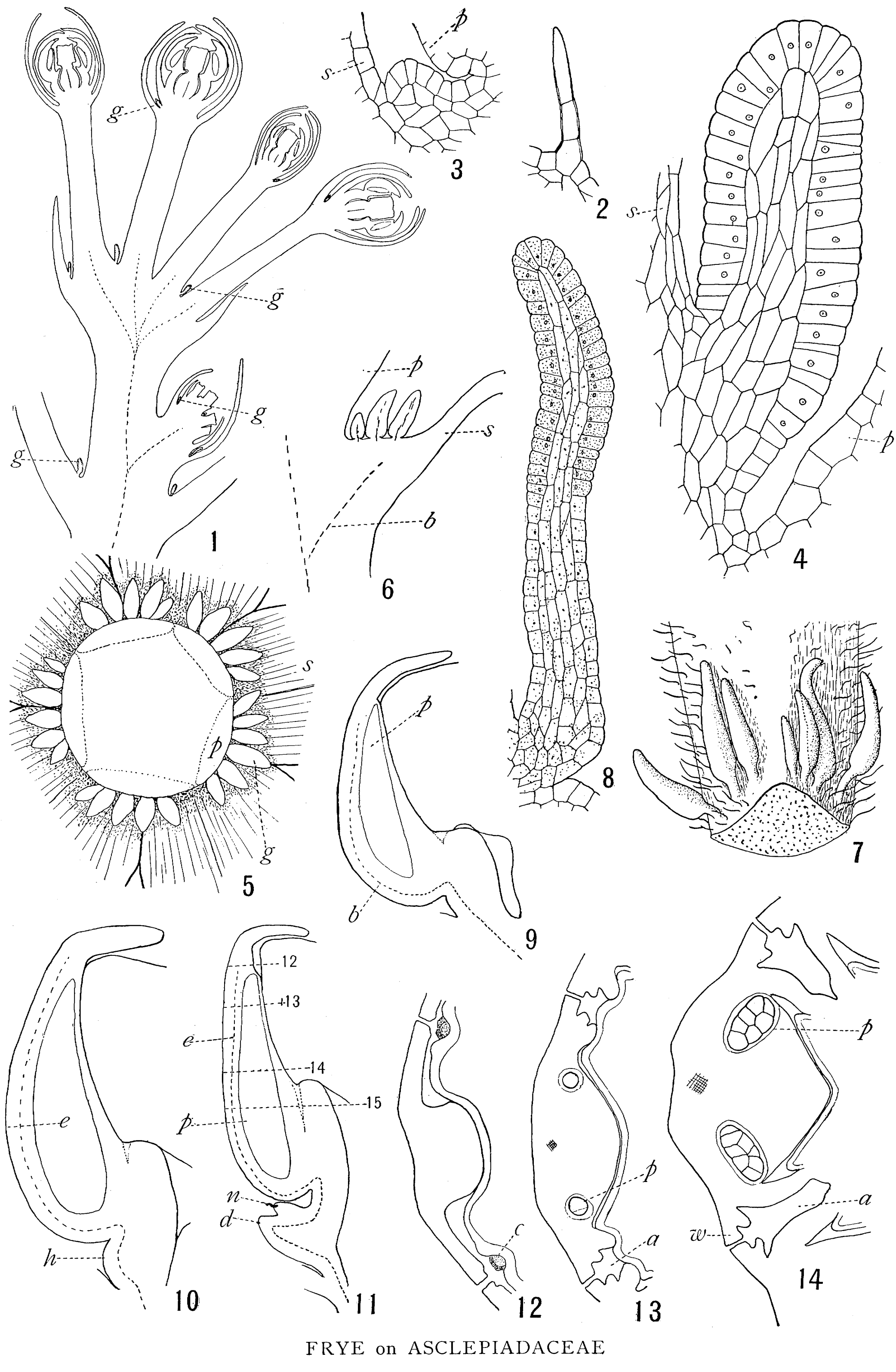
FIG. 27. Two male cells shortly after their formation ; × 2200.

Asclepias tuberosa.

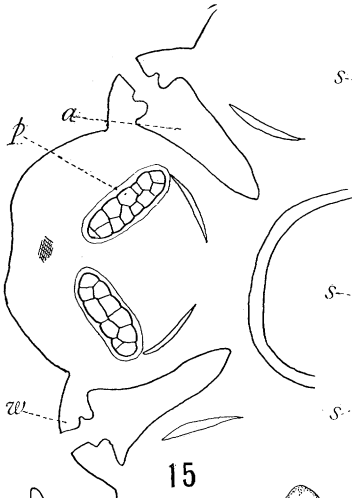
FIG. 28. Longitudinal section of head ; *s*, stigma ; *c*, styler canal ; *g*, glandular epidermis which forms the corpusculum ; *f*, may be functionless stigma ; *t*, conducting tissue ; *b*, bundle ; × 136.

FIG. 29. Ovule with archesporial cell ; × 1275.

FIG. 30. Ovule containing two archesporial cells ; × 2200.



FRYE on ASCLEPIADACEAE



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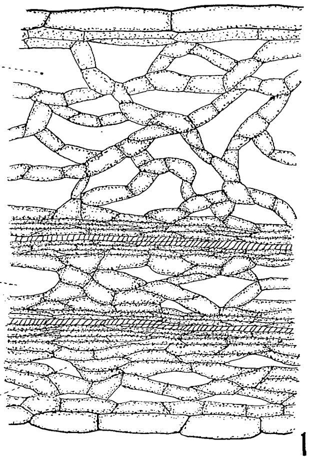

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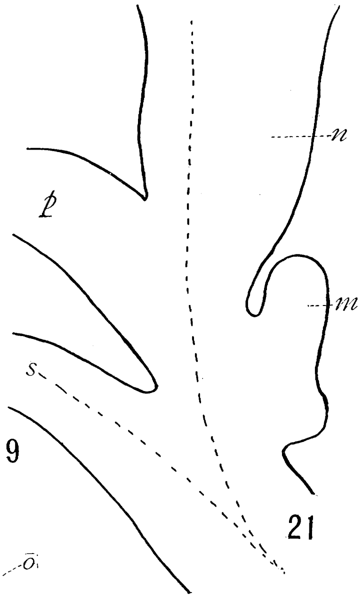

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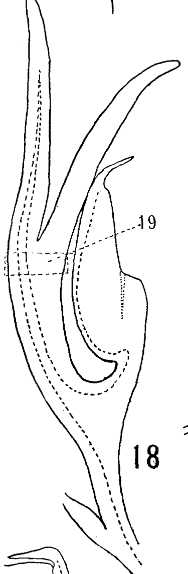

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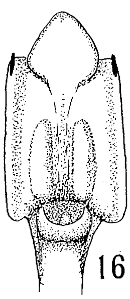
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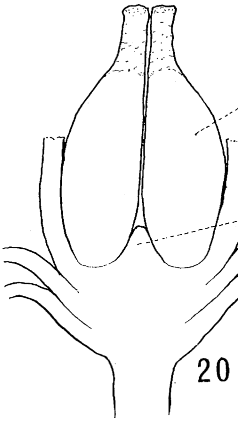

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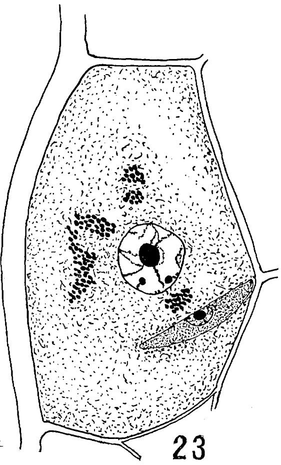
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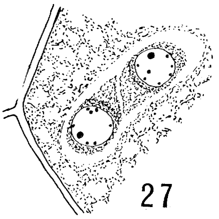
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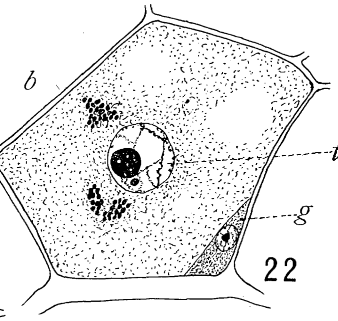

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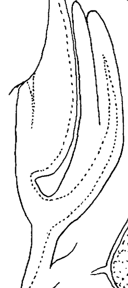
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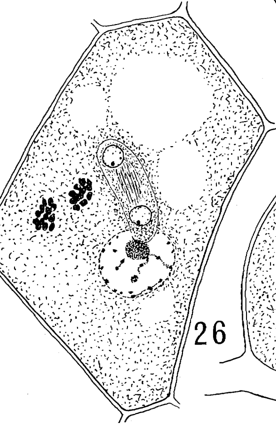
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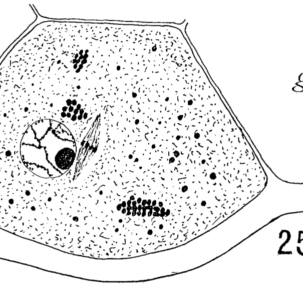
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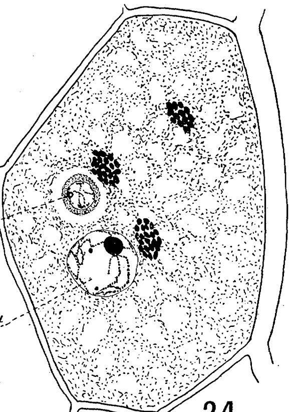

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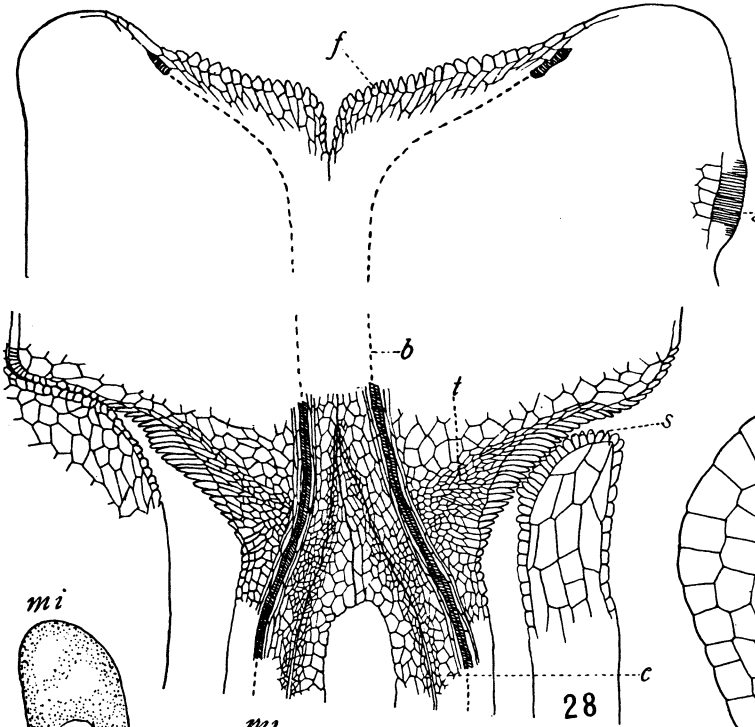

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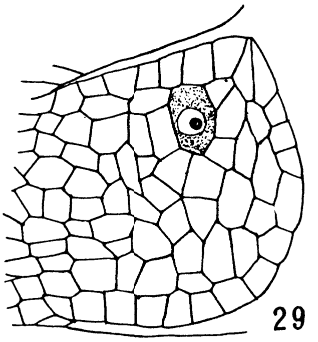

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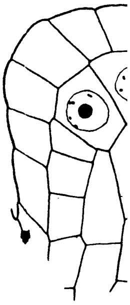

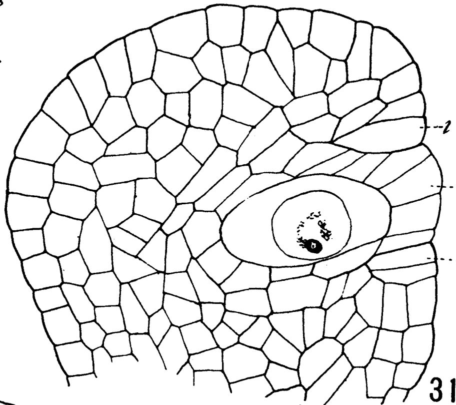

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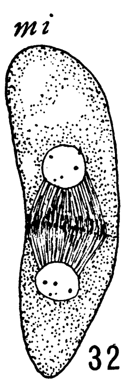

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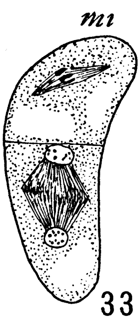

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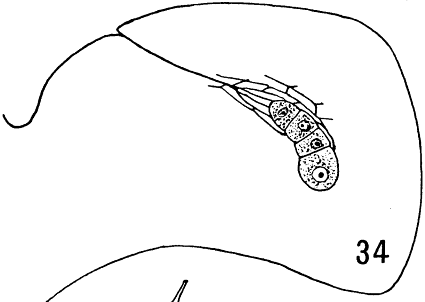

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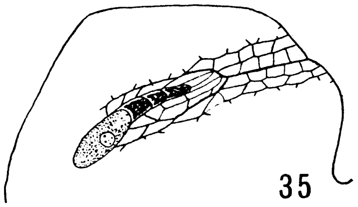

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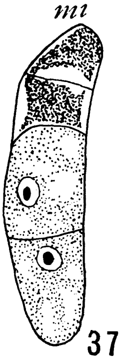

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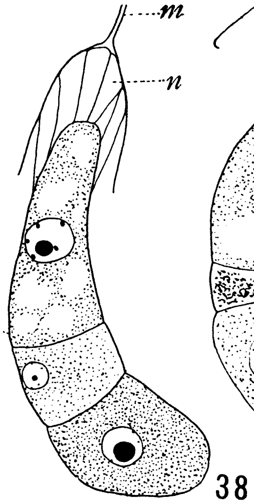

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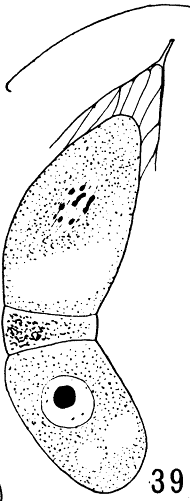

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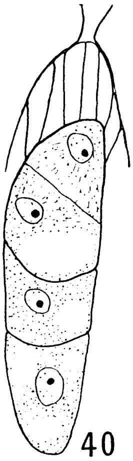

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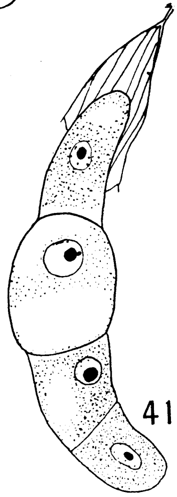

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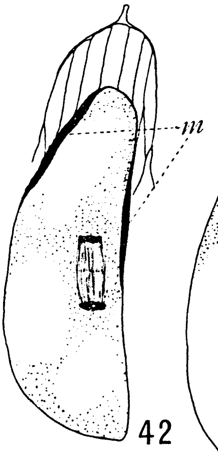

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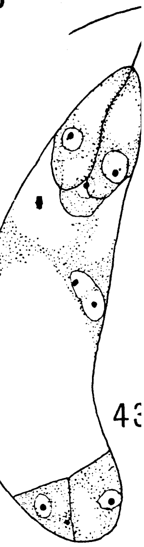
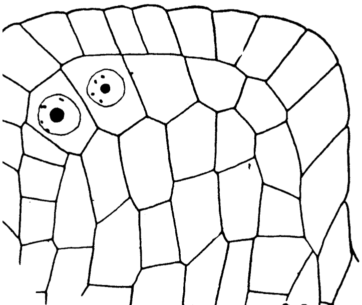


43

FRYE on ASCLEPIADAC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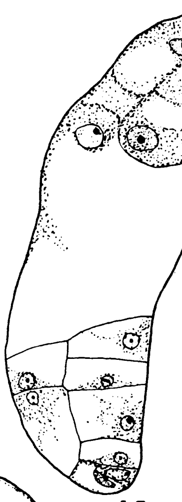
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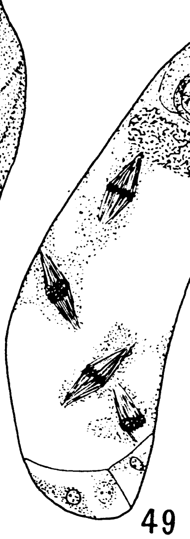
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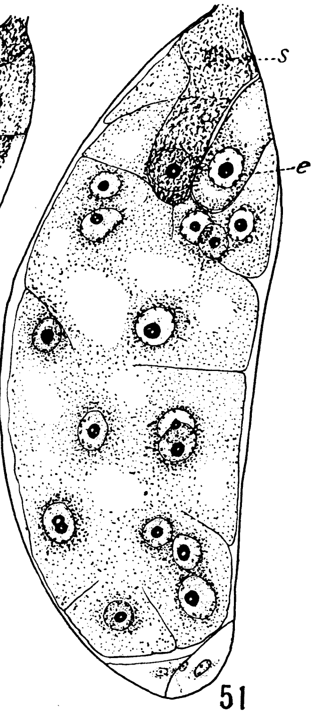

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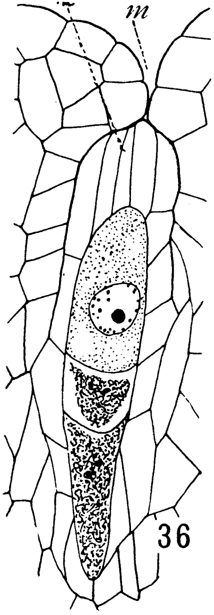

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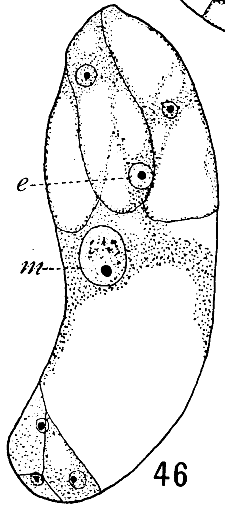

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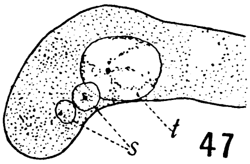

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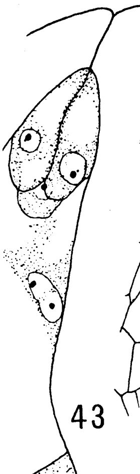
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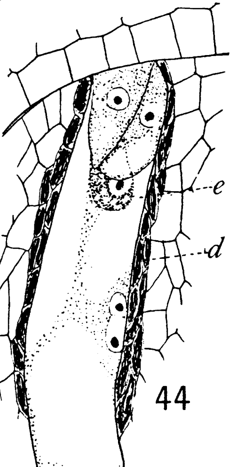

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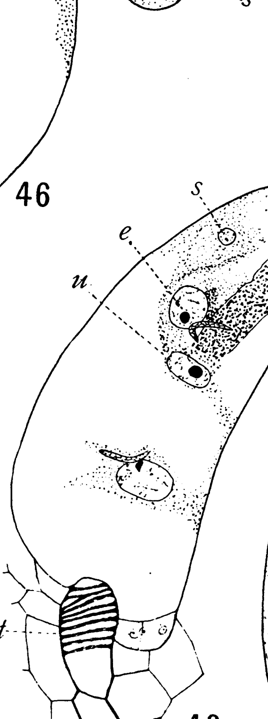

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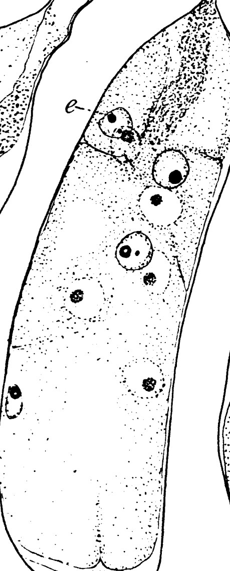

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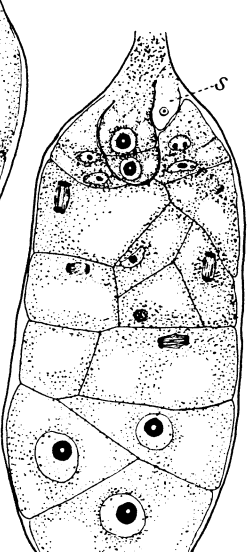

52

EPIADACEAE

FIG. 31. Ovule with integument just beginning to show; *i*, integument; *n*, nucellus; × 1500.

FIG. 32. First division of the mother cell; × 2200.

FIG. 33. Division of the daughter cells; × 2200.

FIG. 34. Row of four megaspores with the fourth surpassing the others; × 780.

FIG. 35. Disorganization of the first three megaspores; × 780.

FIG. 36. Domination of the first megaspore; *n*, nucellus; *m*, micropyle; × 2200.

FIG 37. Row of four megaspores, two of which are about equally active; × 2200.

Asclepias Sullivantii.

FIG. 38. First daughter cell not yet divided; fourth megaspore enlarging; *m*, micropyle; *n*, nucellus; × 2200

FIG. 39. First daughter cell dividing; third megaspore disorganizing; × 2200.

FIG. 40. Division of first daughter cell just completed; × 2200.

FIG. 41. Dominance of the second megaspore; × 2200.

FIG. 42. First division in the embryo sac; *m*, disorganized megaspores; × 2200.

Asclepias tuberosa.

FIG. 43. Normal embryo sac; union of polar nuclei; × 1500.

FIG. 44. Embryo sac which has reached the surface of the ovule; *e*, egg; *d*, disorganizing cells; × 1500.

FIG. 45. Eight antipodals; × 1500.

FIG. 46. Complete union of the polar nuclei before fertilization; *e*, egg; *m*, endosperm nucleus; × 1500.

FIG. 47. Tip of pollen tube entering the stigma; *s*, male cells; *t*, tube nucleus; × 2200.

Asclepias Cornuti.

FIG. 48. Double fertilization; *u*, micropylar polar; *e*, egg; *s*, synergid; *t*, tracheid; × 1500.

FIG. 49. Third division of the endosperm; × 1500.

FIG. 50. Eight-nucleate endosperm; *e*, egg; × 1500.

FIG. 51. Sixteen-celled endosperm; *e*, egg; *s*, synergid; × 1500.

FIG. 52. Two-celled embryo; endosperm massed about embryo; *s*, synergid; × 1085.